

# RAPTOR RESEARCH

A QUARTERLY PUBLICATION OF THE RAPTOR RESEARCH FOUNDATION, INC.

VOL. 20

SUMMER 1986

No. 2

## NOTES ON THE BREEDING CYCLE OF CAPE VULTURES (*Gyps coprotheres*)

ALISTAIR S. ROBERTSON

**ABSTRACT** - Observations were made of the pre-laying, incubation and nestling periods of the Cape Vulture (*Gyps coprotheres*) at a colony in the southwestern Cape Province, South Africa. Some members of the colony were colour-ringed as nestlings; this allowed the sex of breeding partners to be determined by subsequent observation of copulation. Information on occupancy of nest sites, nest-building, a sex-related behavioural difference, dates of egg-laying, incubation and nestling periods, parasite infestation (*Prosimulium* spp.), and associated blood parasites (*Leucocytozoon*) of nestlings is presented.

The Cape Vulture (*Gyps coprotheres*) is the heaviest endemic accipitrid in southern Africa and is the only vulture in the region to breed in colonies on cliff faces (Mundy 1982). Approximately 3500 Cape Vulture nestlings have been colour-ringed (banded) in southern Africa since 1974; studies of marked birds, however, are mostly confined to aspects of dispersal and survival (Houston 1974; Piper et al. 1981; Mundy 1982).

Here I present results of observations made during a case study of a particular colony, to supplement Mundy (1982) and provide information on the behaviour of colour- and metal-ringed breeding adults. Sexes of *Gyps* are morphologically indistinguishable in the field (Houston 1976; Mundy 1982), therefore marked birds provided an opportunity to investigate behavioural differences between sexes, as well as nest-site fidelity (Robertson 1984). The pre-laying, incubation and nestling periods (Newton 1979) are considered separately; observations on the post-fledging dependence period and copulatory behaviour are described elsewhere (Robertson 1983, 1985).

### STUDY AREA AND METHODS

Observations were made at a colony in the Potberg (34° 22' S; 20° 33' E), approximately 10 km from the Indian Ocean coast and approximately 50 km northeast of the southern tip of Africa. About 50 vultures inhabit a ravine of the mountain, and use cliffs facing southeast and southwest for nest and roost sites. In addition, a smaller colony of about 20 at Aasvogelvlei, 120 km from Potberg, was monitored for numbers and breeding success.

The region has a temperate Mediterranean climate and receives most of its rainfall (≈ 530 mm/y) from about May to September (i.e., winter).

All active nest sites and roosting ledges were visible from the southeast side of the ravine, 300-400 m away. Observations were made with binoculars and a 15-60x telescope. Observations began in May 1981, continued for 12 d each month regardless of weather conditions, and ended in May 1982. One "day" represents the time period 0730 H - 1630 H. The concluding stages of the 1980 breeding season, all stages of the 1981 season and the initiation of the 1982 season were covered. Presence of birds at sites and roosting ledges was noted every 30 min during each observation day; the proportion of each class (i.e., one, both or neither occupant present at each count during an observation day) was determined and converted to an arcsine transformation (Scheffler 1969). Although most of the breeding pairs were not individually recognizable, some ringed breeders were present. At a nest where both birds were colour-ringed, strangers alone at the nest for longer than 5 min were seen only 3 times. Unless shown to the contrary, vultures observed at a site were regarded as the occupants. Individual vultures were age-estimated using the characters given by Mundy (1982). At nests where at least one partner was ringed, sex was determined by observation of copulation attempts.

Laying dates for 1981 and 1982 were determined by checking the colony regularly, although precise dates for 3 nests were not obtained in 1982. Dates for 1977, 1979 and 1980 as well as the dates of laying in both 1981 and 1982 at Aasvogelvlei were estimated using an average incubation period of 57 d and a known-age/wing length curve (Mundy 1982). Wing lengths of nestlings measured before 1981 were obtained from unpublished records; thus, only laying dates of sites that produced large nestlings were obtained for years other than 1981 and 1982.

Nestlings at both colonies were colour-ringed, weighed and measured as part of the colour ringing scheme on Cape Vultures (Ledger 1974). Nests were visited on 5 other occasions in order to collect added eggs or shell fragments (measurements in Robertson 1984) and to replace an egg that an adult had knocked from the nest cup. In 1981, nestling blood samples were obtained from both colonies. Smears were prepared following Greiner & Mundy (1979) and scanned for blood parasites by M.B. Markus.

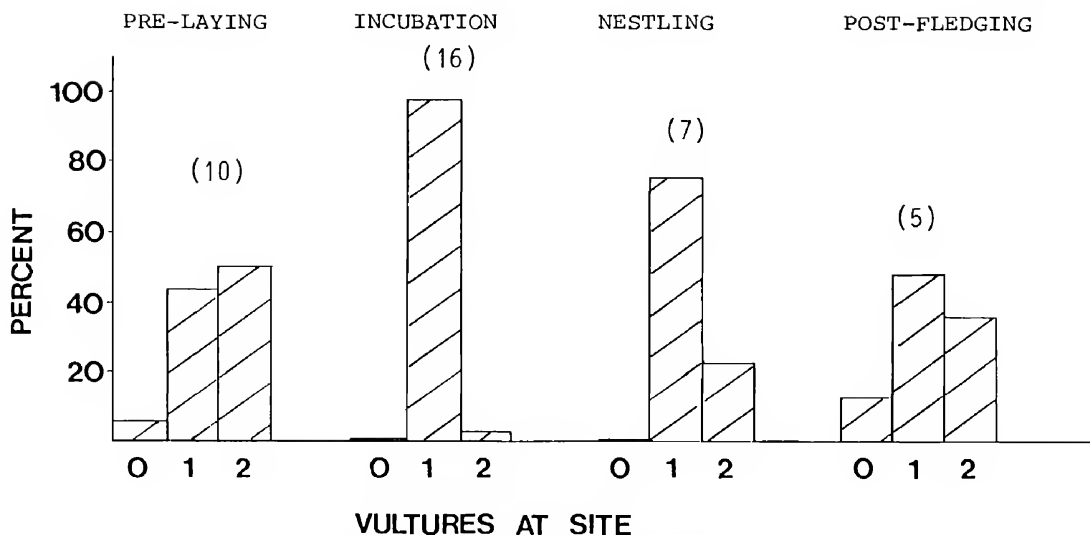


Figure 1: The average level of occupancy of nests during different periods of the breeding cycle. The number of nests used in the calculations for each period is indicated.

## RESULTS

**Pre-laying period.** — Because of the length of the breeding cycle, certain pairs displayed an overlap of post-fledging and pre-laying periods (Robertson 1985). Other pairs that failed in breeding retained their nest site (by aggressively chasing off visitors) from the date of failure.

Figure 1 depicts the average occupancy of 10 nests for the 1981 pre-laying period. On average, nest sites were left vacant for 5% of the observation time.

**(a) Activation of nest sites.** — Of 17 breeding sites active in 1981, 14 were active again in 1982. Of 4 additional nests active in 1982, one was active in 1980. Thus only 3 sites were initiated during the observation period.

At one site on 29 October 1981, 2 birds were seen to stand very close together, facing inwards and picking at sticks on the surface. Seven min later, the ringed female occupant landed at the site and repulsed both, which then repeated this behaviour at another (vacant) site. The impression was of a pair "prospecting" for a possible future breeding site, about 7 months before the next season's average laying date.

At another site, an immature male (est. 3rd y) and female (est. 4th y) were observed to copulate 36 times between 30 June and 30 December 1981. On most occasions after the copulation attempt, both

birds bent over and picked at the nest contents. The nest was examined on 8 October and consisted of a few sticks and green sprays — an "intermediate" nest structure. The first intruder repulsion at this site was observed on 20 December. This site produced a fledgling in 1982/3, thus it was effectively activated in mid-1981, if the parents are assumed to be the same individuals.

A probable mate replacement (certainly the initiation of breeding) occurred at one site in 1983, where a colour-ringed, 6 y old female was observed from late December 1982. This site was active in 1980 and 1981 (both partners adult and unringed). The 6 y old's sex was determined by observation of a copulation attempt with an unknown adult at a perch on 18 May 1982.

**(b) Nest-building.** — No sign of nest-building at any site was observed before the end of March 1982, and at only 2 sites, successful in the previous cycle, were there any remains of the nest structure. By the end of December 1981, nest material on the sites of all failed breeding attempts had disappeared. Collection of nest material in earnest was first observed on 25 April 1982, about 10 wk before the average laying date. Branches comprising the nest structure were collected in most cases from 2 separate areas on the ravine slopes and carried back to the nest in the bill.

At 6 nests where male and female were distinguished, frequency of collecting forays by either sex

was determined. Collecting forays were mainly determined for 3 nests only — those situated on the cliff directly opposite the observation point where the collector's sex was determined with greater certainty. Of 98 collections, males collected 75 times (76%), far more than did females, although at one nest the difference was not so marked. The female generally packed the material into the structure, although both sexes were often seen bending over and rearranging material.

**Incubation period.** — In 1981, 356 nest-d of observation of 16 nests with eggs were made, and I made a further 99 nest-d of observation during an 8-d consecutive period in 1982.

No double clutches (Mundy & Ledger 1975) or replacement clutches were recorded, although the egg at nest #55 was laid 40 d later than the estimated 5 June mean for that year and may thus have been a replacement clutch.

For 16 incubation periods in 1981, which includes one egg lost after 41 d, one adult was at the site at 97.7% of the counts (range 91.2% - 100%).

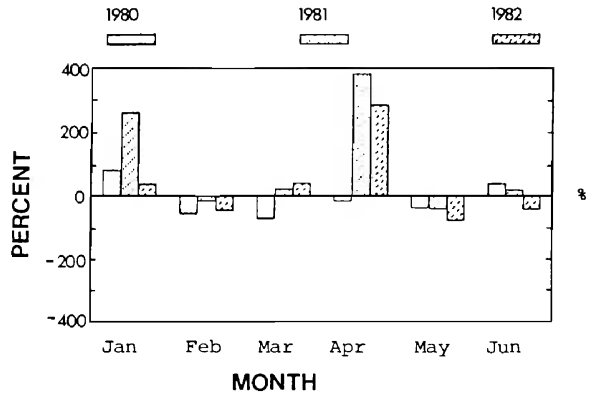


Figure 3: Rainfall in the six months preceding egg-laying, expressed as a percentage deviation above and below the monthly mean.

These sites were unoccupied only 0.09% of this observation period, where an average of 359 thirty-min counts were made per nest. (Fig. 1). On average, 2 birds were at the site 2.0% of the time (range 0% - 8.8%). Birds generally incubated the

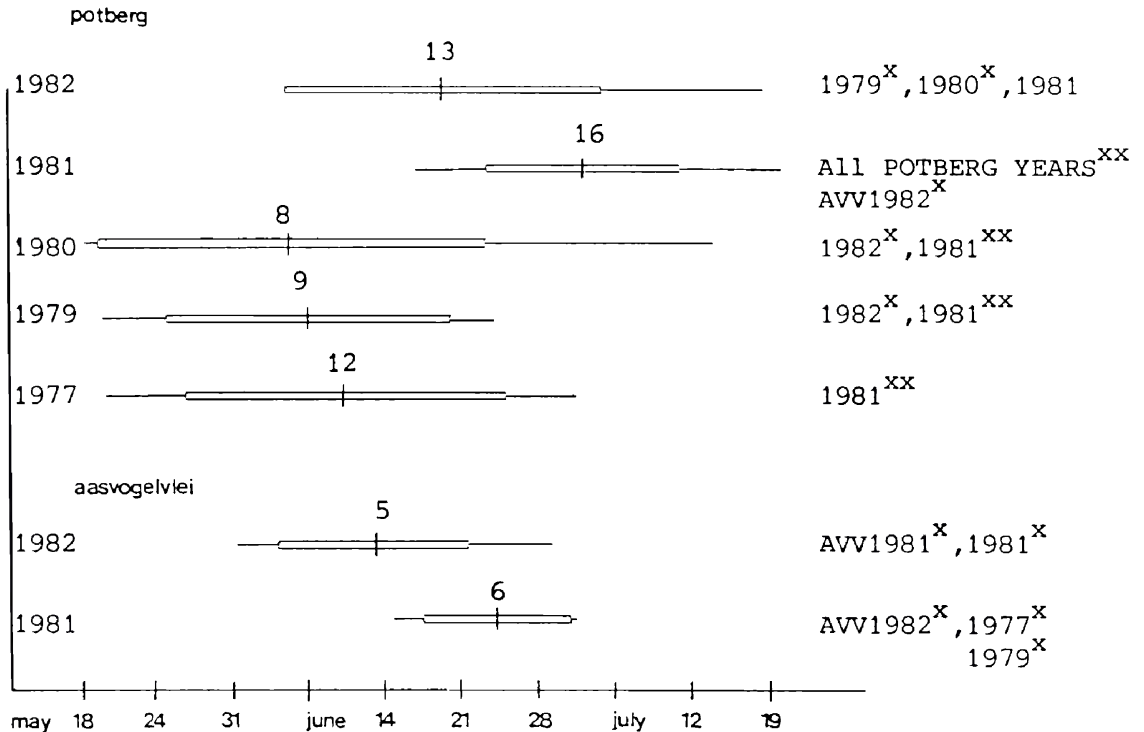


Figure 2: Dates of egg-laying at Potberg and Aasvogelvlei. The mean ( $\pm$  s.d.) and range are shown, as well as significant differences in dates of laying between the various years (0.01 level: year<sup>xx</sup>; 0.05 level: year<sup>x</sup>).

egg very tightly and on only one occasion did an adult leave an egg unoccupied (for 182 min) for no apparent reason.

**(a) Date of laying.** — Only in 1977 did the correlation of higher rainfall and later mean date not occur, although the differences are very slight (compare Figs. 2 and 3). The 1981 mean laying date was significantly later than any other year at Potberg, and similar only to the mean for the same year at Aasvogelvlei (t-Test, 20d.f.,  $P = 0.09$ ). The overall average laying date for the 5 y is 17 June (s.d. = 17.5 d,  $n$  eggs = 58), and this is clearly later than the early-May average for the Skeerpoort, Magaliesberg colony (Mundy 1982) and the similar average for the Collywobbles, Transkei colony (Vernon et al. 1982).

All 1981 eggs were laid considerably later than in 1980, except the likely replacement clutch mentioned. Considering the 3 long, post-fledging dependence periods observed in 1981/2 (Robertson 1985), an egg was laid at the same site before the mean 1981 laying date on one occasion and after it on another; the third site was not active in the subsequent season. After the post-fledging dependence periods observed in 1981/2, eggs were laid at the same sites before the mean 1982 date on 4 of 5 occasions and significantly later by the same adults (colour-ringed) in one instance. At the site with the longest 1981 post-fledging dependence period, the following year's egg was laid before the colony's mean egg-laying date for that year.

The most accurate times of laying were obtained for 3 eggs in 1981, where eggs were laid between 1630 H and 0730 H the next day. At one site (nest #63), the same colour-ringed female laid an egg in 1982 between 1730 H and 1500 H, on exactly the same date as the previous year.

**(b) Changeovers and attentive periods.** — Changeovers (nest relief) occurred within about 3 min of the mate's arrival, although certain partners gave the impression of being "reluctant" to leave. In such cases, changeovers occurred after the incubator had been gently nudged off the nest; this was more frequent during the nestling period. During what was most likely the first changeover at one nest, the incoming adult allowed the egg to roll out of the cup by standing on the rim. After a few feeble attempts at replacing the egg with its bill, it continued to "incubate" the empty nest. During the next 90 min, the bird tried 3 times to replace the egg which lay some 8 cm from the rim. I replaced the

egg at 1540 H, after it had been exposed for 430 min (clear weather, 9-13 knot breeze). This egg subsequently produced a juvenile that fledged. A total of 186 changeovers of birds incubating eggs were noted in 1981, averaging 11.6/site, or 0.5/nest-d of observation. A number of changeovers at outlying sites were probably missed. If the ledge directly opposite the observation point is considered alone, 61 changeovers were documented for 4 incubation periods during 88 nest-d (0.7 changeovers/nest/day). Rarely up to 3 changeovers might occur on the same day. Changeovers occurred in the mornings, before a day's foraging, or in the afternoon after foraging. The earliest time where the incoming partner had fed that morning (bulging crop observed) was 1130 H; if changeovers are then divided into pre-1130 H (61, or 33%) and post-1130 H groups (125, or 67%), then incoming adults had obtained food on 64% of the latter (8.6% cases unknown). The overall average changeover time was 12 hr 54 min, 50 min earlier than that documented for the Skeerpoort, Magaliesberg colony (Mundy 1982:161).

Incubating birds occasionally stood up to stretch, flap their wings, repulse intruders or move the egg (along its long axis, Mundy 1982), and the longest period in such cases that the egg was exposed was 4 min ( $n = 18$ ,  $\bar{x} = 1.2$  min). Attentive periods have been divided into those where 2 changeovers occurred within one observation day ("within-day"), and longer stints. In 1981, the mean "within-day" attentive period was 3 hr 15 min ( $n = 44$ ), which was not significantly different from the 3 hr 31 min period in 1982 (t-Test, 60d.f.,  $P = 0.30$ ). The mean of 1981 "long" attentive periods was 26 hr 21 min ( $n = 72$ ), significantly longer than the 1982 mean of 22 hr 35 min (t-Test, 98d.f.,  $P = 0.01$ ). If 11 abnormally long attentive periods (mean 44 hr 3 min, range 40 hr 45 min - 48 hr 8 min) are excluded, the 1981 mean is not significantly longer than that obtained for 1982 (t-Test, 86d.f.,  $P = 0.37$ ). In 5 of these extra-long cases, the individual concerned was ringed, confirming that no changeover had been missed.

Sexes could be distinguished at 5 nests by the presence of either a metal-ringed (2 nests) or colour-ringed partner. Only when a ring was clearly resighted at both changeovers, were the corresponding attentive periods used in analysis of any sex-related differences. The mean for males (1981 and 1982 values combined) was not significantly

longer than that for females (t-Test, 30d.f.,  $P = 0.32$ ). The frequency of attentive periods by either sex was not significantly different ( $\bar{\chi}^2 =$  expected values ets,  $P = 0.72$ ).

Five eggs failed to hatch in 1981 and 1982. In 2 cases no change in incubation behaviour after the expected hatching date was noted. For example, adults at nest #29 continued to incubate normally for 18 d after the expected hatching date, until I collected the egg. At one nest, however, the incubating adult tended to stand over the egg, rather than sit on it from about 14 d after the expected hatching date. Twenty-four days after the expected hatching date, the incumbent adult deserted this egg for 152 min, returned to stand near it for 355 min, to leave it unattended that night (I collected the egg the next day).

At 6 sites in 1981 where both laying and hatching dates were accurately obtained, the average incubation period was 57 d (95% C.L.'s 55.6 - 58.4).

**Nestling period.** — At 10 sites with nestlings, 377 d of observation were made in 1981, and 15 nest-d at 4 nests in 1982. In 1981, 7 nestlings lived longer than 11 d and 6 fledged, and of 10 nestlings colour-ringed in 1982, 7 fledged (Robertson 1984).

Only 11% of copulation attempts observed at successful sites through the 1981 cycle occurred during the nestling period (Robertson 1983). The mean hatching date for the years 1977 and 1979-1982 was 14 August (using mean laying date of 17 June and a 57-d incubation period).

**(a) Parental care of nestling.** — In 1981, nestlings at 7 nests were left unattended for 1.2% of the counts (range 0.1% - 4.5%). One nestling was unattended for significantly more time than 3 others (Sheffe's tests,  $P < 0.05$ ). Six nestlings were unattended at least once during the period (*i.e.*, one never), and the average age at the first such instance was 71.7 d (range 41-93 d). Nestlings were accompanied by 1 adult on 76.4% of the counts (Fig. 1). Both adults were at the nest on 22.4% of the counts; in all cases attendance by both parents was greater than during incubation.

In 1981 sexes were distinguishable at only one active nest and both partners attended the nestling for similar lengths of time (t-Test, 21d.f.,  $P = 0.43$ ). Both male and female attendance periods were significantly shorter than those obtained during the incubation period (t-Tests,  $P < 0.01$ ).

The mean "long" attendance period of 21 hr 56 min ( $n = 71$ ) was not significantly shorter than the mean for incubation, if the 11 "extra-long" stints are excluded (t-Test, 129d.f.,  $P = 0.09$ ). If these values are included, the difference becomes significant. The mean "within day" attentive period of 3 hr 39 min ( $n = 53$ ) was not significantly longer than the value for the incubation period (t-Test, 95d.f.,  $P = 0.17$ ). The average changeover time was 1229 H, significantly earlier than that documented for the incubation period (t-Test, 375d.f.,  $P = 0.49$ ). Of 193 changeovers, 65.8% occurred after 1130 H and on 86% of these, the incoming adult had obtained food.

For its first few weeks, the nestling was brooded closely by the adult, making the precise time of hatching difficult to discern. There was subsequently a gradation in attendance behaviour of parents, particularly after the nestling was dorsally feathered. A 4-month-old nestling wandered 2 m to an adjacent site containing a 5-month-old nestling on 3 times; both pecked gently at each other's necks before being aggressively jabbed at by an attendant adult. Similar behaviour was never observed for adults of adjacent sites. Parents continued to bring sprays of fresh green leaves to the nest during this period.

Most feeding was bill-to-bill, with the nestling actively calling and tapping the parent's bill. On at least 7 occasions, parents that had not fed were observed to go through the motions of regurgitating seemingly without any food appearing. Nestling development has been described by Mundy (1982), and correlations of wing with body mass and age are presented in Robertson and Boshoff (in press).

**(b) Parasite infestation.** — All nestlings visited on 8 October 1981 were infested with black flies *Prosimulium* spp. (identified by J.S. Paterson). The average age of these nestlings was 43 d (range 22-55 d). The heaviest infestation was on a 47-d-old nestling, where one-half of the head was fully covered (Fig. 4). The main area affected was the crown, but one nestling showed 2 areas of infestation under the wing. The infestation on one nestling, that was unattended while adjacent nestlings were ringed, increased on its head and back, *i.e.*, the presence of the adult (that had flown because of my presence) affected the degree of infestation. This was confirmed later by observing attendant adults removing flies from nestlings with their bills. When



Figure 4: Simuliid infestation (dark area on the otherwise white head) of a 47-day old Cape Vulture nestling.

all nestlings were visited 34 d later, only one fly was observed on the head of an 83-d-old nestling. One 55-d-old nestling had a very low *Leucocytozoon* infection (2 gametocytes in a blood smear); no infection was noted for the same individual in 2 smears taken 34 d earlier. *Plasmodium* spp., microfilariae

and other protozoa were searched for but not found (M.B. Markus *in litt.*).

No simuliids were observed at Aasvogelvlei in either year, and examination of samples from 4 nestlings did not reveal the presence of any blood parasites.

In 1982, less than 10 black flies were present on the crowns of only 2 of 10 nestlings examined.

Figure 5 records the degrees of simuliid infestation for the years 1976-1982, relative to the rainfall for the 6 months before September (data from Boshoff and Currie 1981, unpubl. records).

(c) **Length of nestling period.** — Where no days of observation preceded the day the fledgling was first seen away from the nest, the fledging date was not accurately known (4 cases known to within 5 d). Where at least 2 observation days preceded the date of the first observed flight, that day was taken as the fledging date. In 1981, mean nestling periods were 148.0-150.3 d (range 139-171 d). Both these means were significantly longer than the 1982 mean of 137 d (range 124-147 d) (t-Test for mean of 148, 11d.f.,  $P = 0.04$ ). The individual with the 125-d nestling period was found dead an estimated 3 wk after fledging. The next shortest nestling period was 136 d, and this bird survived at least 5 mo.

The mean for all available nestling periods was 143 d, very similar to Mundy's (1982) estimate of 140 d. The mean 1981 fledging date was 21-23 January 1982, and this contrasts with 28 December for 1982 fledglings.

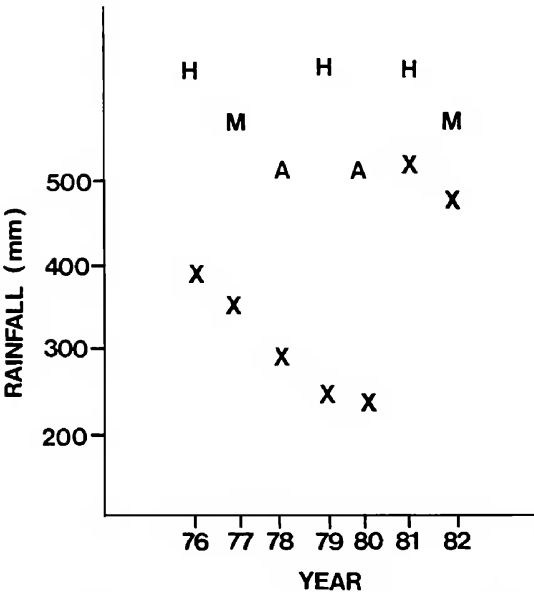


Figure 5: Simuliid presence related to the amount of rain in the six months preceding September. The degree of infestation is classed as heavy (H) (e.g., Fig. 4), medium (M) or absent (A), and the mean amount of rainfall for these months is shown (x).

**DISCUSSION**

**The Pre-laying period.** — Breeding sites are seemingly occupied about 6 mo or more before egg-laying. I can only conclude that pair formation preceded occupancy of a site: single vultures were not seen consistently at the few sites initiated during the study period. I discerned few courtship procedures except, perhaps, mutual preening and scapular action (Berruti 1981). Obviously, many signals perceived by either sex may not be perceived easily by human observers. In the Cape Vulture, pair formation occurs in association with the breeding colony, and specifically the nesting ledges, where 96% of all copulation attempts occurred (Robertson 1983). In contrast to the feeding area which, certainly in this colony's case, is totally man-influenced (Boshoff et al. 1984, Robertson

Table 1: Copulation attempts observed at the Potberg Cape Vulture colony during the study period.

SITE	(A)	(B)	A/B	TOTAL OBSERVED JAN 82 - MAY 82	EGG LAID (E)
	NO. BEFORE EGG LAID	TOTAL OBSERVED MAY 81 - DEC 81			
7	112	113	99.1	38	E
13	31	35	88.6	18	E
16	42	53	79.2	54	E
6	30	39	76.9	34	E
26	49	61	80.3	53	E
4	44	55	80.0	64	E
63	59	59	100.0	22	E
57	44	45	97.8	25	E
17	48	57	84.2	51	E
61	17	30	56.7	54	E
30	38	49	77.5	5	EE
18	39	49	79.6	48	E
57	31	31	100.0	46	E
29	39	57	68.4	4	-
45	21	21	100.0	0	-
3	54	54	100.0	1	-
2	-	32	-	30	E
50	-	8	-	25	E
25	-	24	-	71	E
64	-	0	-	19	E
8	-	117	-	21	-
57 <sup>a</sup>	-	34	-	-	-
Roost Points		56		21	
	Total	1079	Total	704	

and Boshoff in press), the breeding area is unaffected by man. Aspects of breeding behaviour that I observed that are not directly linked to feeding, e.g., nestling attendance and foraging times, might then be representative of the species throughout its range. Because nest material disappeared from some sites before the next season's cycle, the site rather than the nest structure (Newton 1979) would appear to be the more valuable resource.

Houston's (1976) observation of a sex-related difference in behaviour during this period is confirmed; males collected nest material more frequently than females. Such behaviour would reduce the female's energy expenditure; is it then related to production of the egg? Several female

raptors increase in mass before egg production (Newton 1979). However, in the Griffon Vulture that share parental duties, mass increase occurs in both sexes (Houston 1976). Thus energy is accumulated not merely to enable the female to produce eggs, but to supplement the energy budgets of both sexes during the breeding cycle (Newton 1979). Also, the Griffon Vulture clutch of one egg weighs 3-5% of the female's body weight (Mundy 1982) and, in contrast to smaller raptors, makes a relatively small demand on her reserves. Greater male participation in collecting forays may be related to some other factor, such as courtship (akin to gannet behaviour?, see Nelson 1976). In a review of dimorphism in predatory birds, Andersson and

Table 2: Copulation attempts observed per period of breeding cycle. The figures for nest no. 61 are in parentheses as the nestling disappeared before fledging, and the total for successful sites excludes this site.

NEST NUMBER	PRE-LAYING		INCUBATION		NESTLING		POST-FLEDGING		TOTAL NO. COPULATION OBSERVED (E)
	PERIOD A	A/E %	PERIOD B	B/E %	PERIOD C	C/E %	DEPENDENCE PERIOD (D)	D/E %	
6	31	75.6	8	19.5	0	0.0	2	4.9	41
17	47	62.6	8	10.6	20	26.6	0	0.0	75
16	42	38.8	2	1.8	15	13.8	49	45.4	108
18	37	-	1	-	-	-	-	-	38
29	38	-	5	-	-	-	-	-	43
4	44	73.3	0	0.0	13	21.7	3	5.0	60
26	47	-	6	-	-	-	-	-	53
61	16	(59.2)	0	0.0	(11)	(41.7)	-	-	27
30	38	-	0	-	-	-	-	-	38
13	27	-	2	-	-	-	-	-	29
57	30	-	0	-	-	-	-	-	30
55	46	-	0	-	-	-	-	-	46
45	21	-	0	-	-	-	-	-	21
3	45	-	0	-	-	-	-	-	45
63	49	69.0	0	0.0	2	2.9	20	28.2	71
7	112	96.5	0	0.0	3	2.6	1	0.8	116
MEAN		67.8		4.5		15.4		14.0	52.5

Norberg (1981) present hypotheses to account for the lack of (reversed) size dimorphism in colonial carrion feeders; the general lack of sexual differences recorded in this study accords with their predictions.

**Incubation period.** — The timing of egg-laying is apparently not related to success or failure of the previous season's breeding attempt, as indicated at the few sites where juveniles continued to solicit food from parents near the following season's laying date. This suggests that lengthy post-fledging dependence periods may not drain the female's reserves. Whether or not both parents contribute equally to supplying the juvenile with food is unknown, and deserves investigation.

Raptors in general lay earlier in good than in poor food conditions, and food therefore has both a proximate and an ultimate influence (Newton 1979). Long periods of rain or heavy cloud before laying inhibits vultures' foraging and presumably reduces the rate of body reserve accumulation. This could delay laying, and thereby account for the rain-correlated variations in mean laying date. The

markedly regular laying date of particular pairs (identifiable partners at nest #63 had laying dates exactly the same in both study years), however, may point to the operation of other proximate factors. Throughout the Cape Vulture's range there is a gradation in laying dates, from earliest in the Transvaal (early May) through to latest in the southwestern Cape (mid-June).

One should bear in mind that the food source of the Potberg colony is an "artifact" of stock-farming practices. Because the food source has changed markedly within the past century, it is unrealistic to relate overall timing of the colony's breeding cycle to its current food source. Houston (1976) concluded that the breeding season of *G. rueppellii* in East Africa was so timed that the fledging date coincided with a relatively abundant period of food. This link certainly does not hold at Potberg, where nestlings fledge during a time of relative decrease in, but still adequate, food abundance (Robertson and Boshoff in press).

The accurately determined incubation period length of 57 d compares favourably with the 56-d



estimate of Mundy (1982) and the 57.6 d period of Boshoff and Currie (1981). It is clearly longer than the figure given by Brown and Amadon (1968) and McLachlan and Liversidge (1978). Regression equations that compare female weight with incubation periods in a range of raptors (Newton 1979) allow for comparison here: using weights of 8 and 8.5 kg (Mundy 1982), incubation periods of 55 and 56 d are predicted.

**Nestling period.** — Immediately after hatching, both parents usually remained at the nest together for longer periods than during incubation. Nestlings were guarded most of the time by at least one parent (Mundy 1982; this study), unlike other vulture species (Pennycuick 1976; Munday 1982). Predation may account for a substantial portion of egg and nestling loss in colonies, e.g., gulls, reviewed by Hunt and Hunt (1976). The high parental attendance by Cape Vultures, following the period after the nestling is dorsally feathered (and capable of thermoregulation), could reflect an anti-predator response. Mundy (1982) suggested it was an effect of coloniality and the traffic of strangers to the nest. The ability of parents to repulse Black Eagle (*Aquila verreauxi*) predatory attempts is enhanced by their colonial nesting habit (Mundy et al. in press).

That attentive periods of both sexes were shorter than during the incubation period reflects the increased attendance of both parents, as well as less intensive attendance by any one parent. This made changeovers more difficult to discern and resulted in a greater proportion of "within-day" attentive periods being recorded. The earlier changeover time probably reflects the earlier sunrise of approaching summer.

Nestlings of the Lappet-faced Vulture (*Torgos tracheliotus*) are paratized by hippoboscid flies (*Icosta meda*) (Anthony 1976), and in 1981 Potberg nestlings were heavily infested with simuliid flies. Because parents remove flies, the number of flies that I observed was probably greater than it would have been had I not disturbed the parents. The degree of nestling infestation is related to preceding rain as indicated in Fig. 5, although other factors may influence their presence.

Simuliids are known to be vectors of protozoan parasites (Fallis et al. 1973), and are likely vectors of avian haematozoa (Boshoff 1981; Boshoff and Currie 1981). Blood smears of 1979 nestlings (a year of heavy infestation) contained one or more

species of *Leucocytozoon*, the degree of infection varying (Boshoff and Currie 1981). The early blood film taken from a 22-d-old nestling revealed no *Leucocytozoon* presence probably because of aspects of the fly's life cycle: gametocytes of *L. neavei* were first seen in peripheral blood of Helmeted Guineafowl (*Numida meleagris*) nestlings 14 d after infection from sporozoites (Fallis et al. 1973). The subsequent fledging success of those Potberg nestlings is unknown, thus, whether *Leucocytozoon* contributes to Cape Vulture mortality or morbidity remains undetermined. A nestling that exhibited low *Leucocytozoon* infection (and which was fed on by a large number of simuliids) was last seen flying 6 d after it fledged, and it did not have a post-fledging dependence period. Given the necessity of at least some supplementary aid from parents during this period (Robertson 1985), even if it dispersed, the chances are that it did not live long. However, no link between its probable death and parasitaemia is suggested; the nestling certainly lived for about 3 mo with this infection. More observations of the fate of nestlings infected with blood parasites are needed before effects of either parasite can be determined. Adults remove flies with their bills, suggesting that they are behaviourally adapted to their parasites (Markus 1974). In a previous study of haematozoa from southern African vultures, the Cape Vulture was the only species not infected with blood parasites (Greiner & Mundy 1979). This was ascribed to its unique nesting habit as well as the timing of its breeding season. In their first few weeks of life, nestlings have a relatively soft skin and are either naked or sparsely covered with feathers; consequently it is at this stage they are most vulnerable to biting insects (Markus 1974). Greiner and Mundy (1979:152) sampled nestlings from summer-rainfall colonies, during which time "appropriate ornithophilic vectors are evidently scarce or absent . . . precluding transmission of potential pathogens . . ." Simuliid flies require water in which to breed (Ledger 1979), and the stream in the ravine provides suitable habitat. The Potberg colony is the only one I know of with a suitable breeding ground for these flies within 400m of the breeding ledges (see Mundy 1982; Tarboton and Allan 1984).

The length of the nestling period, although variable between years, is also closely predicted by Newton's (1979) regression equation: 141-148 d for body masses of 8 and 8.5 kg.

## ACKNOWLEDGMENTS

I thank Miles Markus for analysing the blood smears, André Boshoff, Peter Mundy and Hugh Paterson for criticizing the dissertation from which this paper is drawn, and Gordon Maclean, Dave Ward and a referee for comments on drafts. During the fieldwork, I was employed by the Cape Department of Nature and Environmental Conservation and, in 1983, received bursaries from the CSIR and the University of the Witwatersrand.

## LITERATURE CITED

- ANDERSSON, M. AND R.A. NORBERG. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biol. J. Linn. Soc.* 15:105-130.
- ANTHONY, A.J. 1976. The Lappet-faced vultures of the Gonarezhou. *Bokmakierie* 28:54-57.
- BERRUTI, A. 1981. Displays of the sooty albatrosses *Phoebastria fusca* and *P. palpebrata*. *Ostrich* 52:98-103.
- BOSHOFF, A.F. 1981. Notes on two Cape Vulture colonies in the southwestern Cape Province, South Africa. *Vulture News* 5:3-10.
- BOSHOFF, A.F. AND M.H. CURRIE. 1981. Notes on the Cape Vulture colony at Potberg, Bredasdorp. *Ostrich* 52:1-8.
- BOSHOFF, A.F., A.S. ROBERTSON AND P.M. NORTON. 1984. A radio-tracking study of an adult Cape Griffon Vulture *Gyps coprotheres* in the southwestern Cape Province. *S. Afr. J. Wildl. Res.* 14:73-78.
- BROWN, L.H. AND D. AMADON. 1968. Eagles, hawks and falcons of the world. Feltham: Country Life.
- DRENT, R.H. AND S. DAAN. 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* 68:225-252.
- FALLIS, A.M., R.L. JACOBSON AND J.N. RAYBOLD. 1973. Haematozoa in domestic chickens and Guinea Fowl in Tanzania and transmission of *Leucocytozoon neavei* and *Leucocytozoon schoutedeni*. *J. Protozool.* 20:438-442.
- GREEN, R. 1976. Breeding behaviour of Ospreys *Pandion haliaetus* in Scotland. *Ibis* 118:475-490.
- GREINER, E.C. AND P.J. MUNDY. 1979. Haematozoa from southern African vultures, with a description of *Haemoproteus janovyji* sp. n. *J. Parasitol.* 65:147-153.
- HINDE, R.A. 1970. Animal Behaviour. 2nd ed. New York: McGraw-Hill.
- HOUSTON, D.C. 1976. Breeding of the White-backed and Ruppell's Griffon Vultures, *Gyps africanus* and *Gyps rueppellii*. *Ibis* 118:14-40.
- HOUSTON, D.C. 1974. Mortality of the Cape Vulture. *Ostrich* 45:57-62.
- HUNT, G.L. AND M.W. HUNT. 1976. Gull chick survival: the significance of growth rates, timing of breeding and territory size. *Ecology* 57:62-75.
- LACK, D. 1954. Ecological adaptations for breeding in birds. London: Methuen.
- LEDGER, J.A., 1974. Colour rings for vultures. *Safring News* 3:23-28.
- . 1979. African insect life, rev. end. Cape Town: Struik.
- MARKUS, M.B. 1974. Arthropod-borne disease as a possible factor limiting the distribution of birds. *J. Parasitol.* 4:609-612.
- MCLACHLAN, G.R. AND R. LIVERSIDGE. 1978. Roberts birds of South Africa, 4th edition. Cape Town: John Voelker Bird Book Fund.
- MUNDY, P.J. 1982. The comparative biology of southern African vultures. Johannesburg: Vulture Study Group.
- MUNDY, P.J. AND J.A. LEDGER. 1975. Notes on the Cape Vulture. *Honeyguide* 83:22-28.
- NELSON, J.B. 1976. The breeding biology of Frigate birds. *Living Bird* 14:113-155.
- NEWTON, I. 1979. Population ecology of raptors. Berkhamsted: Poyser.
- PENNYCUICK, C.J. 1976. Breeding of the Lappet-faced and Whiteheaded Vultures (*Torgos tracheliotus* Forster and *Trigonoceps occipitalis* Burchell) on the Serengeti Plains. *E. Afr. Wildl. J.* 15:67-84.
- PIPER, S.E., P.J. MUNDY AND J.A. LEDGER. 1981. Estimates of survival in the Cape Vulture *Gyps coprotheres*. *J. Anim. Ecol.* 50:815-825.
- ROBERTSON, A.S., 1983. The feeding ecology and breeding success of a Cape Vulture colony in the southwestern Cape Province. Unpubl. M.Sc. Thesis. Johannesburg, University of the Witwatersrand.
- . 1984. Aspects of the population dynamics of Cape Vultures. *Ostrich* 55:196-206.
- . 1985. Observations on the post-fledging dependence period of Cape Vultures. *Ostrich* 56:58-66.
- ROBERTSON, A.S. AND A.F. BOSHOFF (in press). The feeding ecology of Cape Vultures *Gyps coprotheres* in a stock-farming area. *Biol. Conserv.*
- SCHAEFLER, W.C. 1969. Statistics for the Biological Sciences. London: Addison-Wesley Publishing Company.
- STEYN, P. 1982. Birds of prey of southern Africa. Cape Town: David Philip.
- TARBOTON, W.R. AND D.G. ALLAN. 1984. The status and conservation of Birds of Prey in the Transvaal. Pretoria: Transvaal Museum Monographs no. 3.
- VERNON, C.J., S.E. PIPER AND D.M. SCHULTZ. 1982. The breeding success of Cape Vultures at Collywobbles, Transkei, 1981. *Vulture News* 8:26-29.

Department of Zoology, University of Witwatersrand, Johannesburg 2001, South Africa. Present address: Department of Zoology, University of Natal, Pietermaritzburg 3200, South Africa.

Received 20 May 1985; Accepted 15 September 1985.